Field Observations of Intraspecific Agonistic Behavior of Two Crayfish Species, *Orconectes rusticus* and *Orconectes virilis*, in Different Habitats

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Abstract. Agonistic behavior is a fundamental aspect of ecological theories on resource acquisition and sexual selection. Crustaceans are exemplary models for agonistic behavior within the laboratory, but agonistic behavior in natural habitats is often neglected. Laboratory studies do not achieve the same ecological realism as field studies. In an attempt to connect laboratory results to field data and investigate how habitat structure affects agonistic interactions, the nocturnal behavior of two crayfish species was observed by scuba diving and snorkeling in two northern Michigan lakes. Intraspecific agonistic interactions were analyzed in three habitats: two food resources—macrophytes and detritus—and one sheltered habitat. The overall observations reinforce the concept that resources influence agonistic bouts. Fights in the presence of shelters were longer and more intense, suggesting that shelters have a higher perceived value than food resources. Fights in the presence of detritus patches had higher average intensities and ended with more tailflips away from an opponent, suggesting that detritus was a more valuable food resource than macrophytes. In addition, observations of aggressive behavior within a natural setting can add validity to laboratory studies. When fights in nature are compared with laboratory fights, those in nature are shorter, less intense, and less likely to end with a tailflip, but do show the fundamental fight dynamics associated with laboratory studies. Extrinsic and intrinsic factors affect intraspecific aggression in many ways, and both should always be recognized as having the potential to alter agonistic behavior.

Introduction

Many observations of crayfish behavior have been made under controlled laboratory conditions. These studies generally focus on intraspecific aggressive behavior in terms of shelter acquisition (Capelli and Hamilton, 1984; Peeke *et al.*, 1995; Figler *et al.*, 1999), chemical communication (Bovbjerg, 1956; Zulandt Schneider *et al.*, 1999, 2001), mating (Hill and Lodge, 1999), food preferences (Capelli and Munjal, 1982), and starvation (Hazlett *et al.*, 1975; Stocker and Huber, 2001). Laboratory experiments have been invaluable in clarifying the extrinsic and intrinsic factors that affect agonistic interactions. Intrinsic factors that have been shown to affect aggression are size, sex, reproductive state, hunger state, and social experience, while extrinsic factors are status and individual recognition, resource availability, prior residence, and shelter presence.

Asymmetries in fighting ability may be produced by some intrinsic features or extrinsic circumstances that favor one contestant (Parker, 1974; Maynard Smith and Parker, 1976). Intrinsic asymmetries are accurate predictors of dominance during interactions between pairs of decapod crustaceans; they include physical body size (Bovbjerg, 1953, 1970; Rubenstein and Hazlett, 1974; Berrill and Arsenault, 1984; Pavey and Fielder, 1996), chelae size (Garvey and Stein, 1993; Rutherford *et al.*, 1995), and sex (Stein, 1976; Peeke *et al.*, 1995, 1998). Extrinsic asymmetries such as prior residence (Peeke *et al.*, 1995, 1998), differing fight strategies (Guiasu and Dunham, 1997), and previous history in agonistic encounters (Rubenstein and Hazlett, 1974; Daws *et al.*, 2002; Bergman *et al.*, 2003) contribute to the outcome of agonistic interactions. Seasonal variations in food availability can also increase activity levels that lead to

increased social contact and consequently to increased aggressive interactions (Hazlett *et al.*, 1975). Laboratory experiments are an invaluable aid to understanding behavioral mechanisms, but they have limitations in their applicability to natural ecosystems (Bovbjerg, 1953, 1956; Peeke *et al.*, 1995). One severe constraint on laboratory studies of aggression is the restriction of space, which reduces an animal's ability to escape from an opponent.

Dominance hierarchies, territorial defense, mate selection, substrate preferences, and escalation of fight behavior observed under laboratory conditions may not be representative of behaviors in a natural setting (Karnofsky *et al.*, 1989). These changes in agonistic behavior observed within the laboratory may largely be caused by an inability to escape an agonistic conflict (Hediger, 1950). To circumvent this artifact, studies have been conducted in artificial ponds or streams that are less restrictive than the aquaria used in standard laboratory experiments. By increasing the complexity of the experimental environment, studies in these semi-natural settings attempt to obtain a more natural repertoire of behavior. They provide useful information about agonistic interactions, foraging, mating, orientation, shelter acquisition, and molting (Abrahamsson, 1966; Ranta and Lindström, 1992; Tomba *et al.*, 2001). However, even studies in semi-natural environments cannot illustrate the "true" behavioral ecology of the crayfish. Because of this shortcoming, field studies are invaluable to the understanding of crayfish behavior. They minimize laboratory bias and allow for an integration of behaviors observed in laboratories with those in a natural setting.

Crustaceans, particularly crayfish, have been used as a model system to study aggression (Dingle, 1983; Hyatt, 1983) because of the ritualized nature of their agonistic bouts (Bruski and Dunham, 1987), the presence of formidable chelipeds (Garvey and Stein, 1993; Schroeder and Huber, 2001), and the use of sensory information during such encounters (Zulandt Schneider *et al.*, 1999, 2001; Bergman *et al.*, 2003). The ultimate goal of any aggressive encounter is to obtain an elevated social status that gives an individual an advantage in obtaining a resource, such as food, mates, and shelters (Wilson, 1975; Atema, 1986). Conversely, a subordinate individual may lose access to resources through unsuccessful bouts, but may obtain a net benefit by avoiding costs such as increased energy expenditure, injury from a conspecific, or increased predation risk (Wilson, 1975; Edsman and Jonsson, 1996). If a subordinate does not gain a benefit, then the lower status will have a negative effect on fitness. Consequently, a subordinate will have less food and shelter and fewer mating opportunities.

Extrinsic environmental factors can have a profound effect on aggressive activities; thus a connection between extrinsic factors in the laboratory and their effects in nature need further validation. Agonistic behavior has been studied extensively in the laboratory and in semi-natural conditions, but less emphasis has been placed on agonistic behavior in a natural setting. For this reason, we examined agonistic behavior under natural nocturnal conditions in two northern Michigan lakes. The study was conducted in three different habitats within the lakes to provide a global view of intraspecific agonistic behavior in nature that could be correlated to laboratory results on aggression. The results of this study also allowed us to examine differences in agonistic behavior that may be correlated to differing extrinsic factors in the laboratory and nature.

Materials and Methods

Study site

The study was sited in two remnant glacial lakes in the northern part of the lower peninsula of Michigan: Douglas Lake (lat. 45°33' N, long. 84°57' W) and Burt Lake (lat. 45°28' N, long. 84°40' W). The Burt Lake substrate is predominantly sand and small gravel. Water depth ranges from 0.4 (shallow) to 2.0 m (deep). A mixture of sand and gravel containing intermittent patches of detritus dominates the shallow-water substrates. The deep water contains a sand substrate with a population of macrophytes (dominated by *Potamogeton* sp. and *Vallisneria* sp.) and their associated epiphytes. Water temperatures range from 14 to 23 °C. Observation points were accessed by snorkeling. The Douglas Lake substrate is sand that contains a small band of iron substrata forming natural holes that crayfish use as shelters (burrows). This site ranges from 7.5 to 18.0 m in depth and is devoid of macrophytes. The water temperature ranges from 10 to 15 °C. Observation points were accessed through scuba diving.

Study animals

Both the Burt Lake and Douglas Lake sites contained two species of crayfish, *Orconectes rusticus* and *Orconectes virilis*. Crayfish species were determined by the color of the periopods (chelae and legs), which are bright blue in *O. virilis* and brownish-green in *O. rusticus*. The determination of species allowed for an analysis of conspecific fights. In Douglas Lake, only *O. rusticus* conspecific fights were observed in the shelter habitat. In the Burt Lake population conspecific interactions for *O. virilis* were observed only on the macrophyte beds and not on the detritus patches, even although both species were present in the two regions. The observers took care to avoid physically disturbing any of the animals; they remained as motionless as possible by using intermittent kick strokes to drift over the observation areas (Karnofsky *et al.*, 1989). None of the animals were handled before or captured after behavioral observations. Consequently, male and female crayfish could not be distinguished when aggressive interactions were analyzed, but the relative size difference between crayfish was determined on

a video screen (Sony Trinitron color monitor: model # PVM-1315Q) by calculating the percent size difference of the opponents.

Behavioral observation

Observations were made during July and August between the hours of 2230 and 0100 (nocturnal activity period) from 1996 to 2002 (no observations were made in the summer of 1999). All observations were made on clear, calm nights when the water surf was below 8.0 cm. Interactions were recorded on a video camera (Sony Hi-8 Handycam; model # CCD-TR700) that was illuminated with white lights mounted on an underwater housing (Stingray video housing; model # SR-700) that contained the camera. Animals were filmed from a minimum distance of 0.4 m. Slow swimming motions were made to follow animals, and when the lights on the underwater housing noticeably disturbed an animal, the interaction was removed from the analysis. Crayfish are primarily nocturnal animals, and any behavioral alterations caused by the sudden exposure to white light could not be determined from this study. For this reason, any animal that tailflipped away or used a meral spread in the absence of an interaction was removed from the data analysis; however, this does not take into account any unnoticeable changes in behavior in response to the artificial light. Crayfish do appear to alter their behavior when light intensities are altered (Bruski and Dunham, 1987); however, since uniform white lighting was used in all observations, there should be no differential effects on the behavior.

Two sampling techniques were used. The first technique was to follow a single crayfish until it had an agonistic interaction with a conspecific. The second method was to scan detritus patches (Burt Lake), macrophyte beds (Burt Lake), and the shelter areas (Douglas Lake) for two crayfish that were within two body lengths of one another. When agonistic interactions were observed with either of these sampling techniques, the encounter was videotaped from initiation to termination of the fight and the interactions were later analyzed by playing the tape on a Panasonic VHS recorder (model # AG-7530-P) onto the Sony Trinitron monitor.

Analysis of fight behavior

All videotaped fight trials were analyzed using an ethogram modified from Bruski and Dunham (1987) (Table 1). An agonistic encounter in a laboratory setting with no resources available typically begins when an individual approaches a potential opponent (intensity 1). The encounter may then progress to a series of agonistic threat displays using a meral spread (intensity 2). If neither individual retreats, the bout gradually increases in fight intensity, starting with chelae contact and progressing to pushing with

Table 1

Crayfish ethogram codes

Intensity Level	Description
−2	Tailflip away from opponent or fast retreat
−1	Slowly back away from opponent
0	Ignore opponent with no response or threat display
1	Approach without a threat display
2	Approach with threat display using meral spread and/or antennal whip
3	Initial claw use by boxing, pushing, or touching with closed claws
4	Active claw use by grabbing opponent with open claws
5	Unrestrained fighting by grasping and pulling opponent's claws or appendages

closed chelae (intensity 3). When the chelae are opened and used to grab an opponent, a new intensity level is reached (intensity 4). The most intense interactions have periods of unrestrained fighting in which an individual appears to attempt to injure an opponent by grasping at chelae, legs, or antennae (intensity 5). A conflict is concluded when one individual retreats (intensity −1), usually signified by a tailflip away from the opponent (intensity −2), and usually followed by a submissive posture (Bruski and Dunham, 1987). A subordinate will retreat consistently and assume a posture in which the cephalothorax, abdomen, and claws are near the substrate. Typically, crayfish did not respond to each other when separated by greater than two body lengths (intensity 0). The temporal dynamics of these changes in behavior were recorded to include the total duration of the encounter and the time it took to reach the different intensity levels. Duration, time to different intensities, maximum intensity level reached, and average maximum intensity levels were analyzed using a one-way MANOVA and a Tukey honestly significant difference (hsd) *post hoc* test. The retreating animals (tailflip away) and maximum intensity achieved during an encounter were recorded and analyzed using a multiple comparisons for proportions contingency table ($q_{0.05,\infty,4} = 3.633$) that allows for testing analogous to the Tukey or Student-Newman-Keuls tests (Zar, 1999). Significant results are represented by giving a $q_{0.05,\infty,4}$ value > 3.314 from the multiple comparisons test and a P value < 0.05. An additional power analysis (Power $= 1 - \beta$) was included for the ANOVA and multiple comparisons for proportions contingency table tests. The size differences of agonistic opponents were obtained in 117 of the fights. Size differences are presented as a percentage of the larger animal in the pairing. Thus, a value of 20% means that the smaller animal is 20% smaller than the larger animal. A regression analysis between size difference in percentage and fight duration was analyzed using an exponential regression using the least-squares method.

Results

Qualitative description of fight dynamics

In general, as in the laboratory, crayfish quickly approached one another and immediately began to interact (Bruski and Dunham, 1987; Bergman *et al.*, 2003). In most instances, fights, unlike those in the laboratory, were relatively short and did not always show a stepwise progression in intensities (Stocker and Huber, 2001; Zulandt Schneider *et al.*, 2001; Bergman *et al.*, 2003). Crayfish retreated quickly from opponents by moving away in a different direction. Fights rarely progressed to the high intensities seen in the laboratory (Stocker and Huber, 2001; Bergman *et al.*, 2003), but did seem to include many of the stereotypical agonistic behaviors (Huber and Kravitz, 1995). Surprisingly, the number of fights ending in tailflips was low (45%) compared to fights in a laboratory (>90% for laboratory fights; Moore, pers. obs.). In addition, multiple interactions between the same opponents within a short time were virtually nonexistent, which may be due to social recognition (Daws *et al.*, 2002).

Quantitative description of all fights

Two hundred and forty-six encounters were included in the data analysis. Statistical tests were performed on conspecific fights for *O. rusticus* for the three habitat types. Conspecific fights for *O. virilis* were observed only in the macrophyte habitat, and all statistical tests were done on these animals. Within the macrophyte bed habitat, no significant differences were found for any of the following statistical tests. For this reason, the data for the macrophyte habitat fights were pooled to provide a more global description of the parameters of average agonistic encounters in nature. In the subsequent statistical tests, encounters were separated on the basis of the habitat in which the encounter occurred. The mean duration of all encounters was 5.3 ± 0.4 s (mean $\pm$ SE); ($n = 246$; Fig. 1A), and 0.45 (111 of 246 encounters) of the conflicts ended with the behavior "tailflips away from an opponent" (Fig. 2). Intensity 2 was reached in 0.49 of the encounters (121 of 246; Fig. 3A), intensity 3 was reached in 0.39 (95 of 246; Fig. 3A), and intensity 4 was reached in 0.12 (29 of 246; Fig. 3A). The average maximum intensity of all encounters was 2.6 ± 0.04 on the crayfish ethogram scale (Table 1; Fig. 3B). The rate of escalation is a measure of time to different levels of intensity and averaged 1.5 ± 0.1 s for escalation to intensity 2 (246 of 246 encounters; Fig. 4), 3.9 ± 0.2 s to intensity 3 (124 of 246 encounters; Fig. 4), and 9.5 ± 0.9 s to intensity 4 (28 of 246 encounters).

Fight duration

The overall fight duration in the three habitats for the collective pool of crayfish showed a significant difference
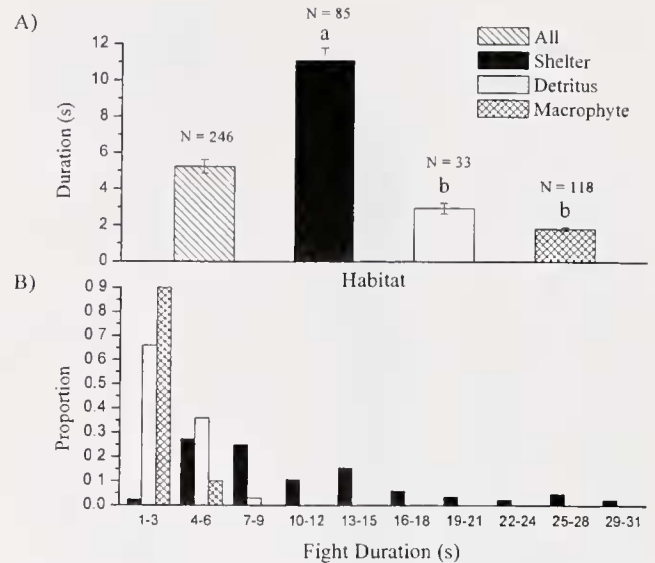

Figure 1. (A) The mean ($\pm$SEM) fight duration of all fights (hatched), fights near shelters (black), fights on detritus patches (white), and fights among macrophytes beds (crosshatch). Values above bars (N =) indicate numbers used for the statistical calculations. The letters above the bars denote a significant difference between the habitat types (one-way ANOVA, Tukey-hsd *post hoc* test; $P < 0.05$). (Note: Nine interactions were not categorized into a habitat type and are only included in the "All" category). (B) Frequency histogram showing the proportion of fight durations in the shelter, macrophyte, and detritus habitats in 3-s bins.

using a one-way MANOVA with a Tukey *post hoc* analysis (Fig. 1A). The fight duration in the shelter habitat (11.1 ± 0.7 s; $n = 85$) significantly differed from both the detritus patch (2.9 ± 0.3 s; $n = 33$) and macrophyte bed interactions (1.8 ± 0.1 s; $n = 118$; Power = 1.00) ($P < 0.05$). There was no significant difference in fight duration between the conflicts occurring on detritus patches and on macrophyte beds ($P > 0.05$). Fight durations for encounters in the shelter habitat ranged between 1 and 31 s, whereas the duration of encounters on macrophyte beds and detritus patches did not exceed 6 s (Fig. 1B).

Tailflip-away

A contingency table for multiple comparisons of proportions demonstrated that agonistic encounters ended in a tailflip significantly more often when the fight was in the shelter ($61/85 = 0.72$; $q = 19.01$; Power = 0.84) and detritus patch habitats ($20/33 = 0.61$; $q = 10.36$; Power = 0.14) than when in macrophyte bed habitats ($30/118 = 0.25$; Power = 0.98) ($P < 0.05$; Fig. 2). No significant difference was found between conflicts in the shelter and detritus habitats ($q = 3.29$; $P > 0.05$).

Fight intensity

A significantly greater proportion of agonistic encounters on macrophyte beds (0.85; Power = 1.00) reached a max-
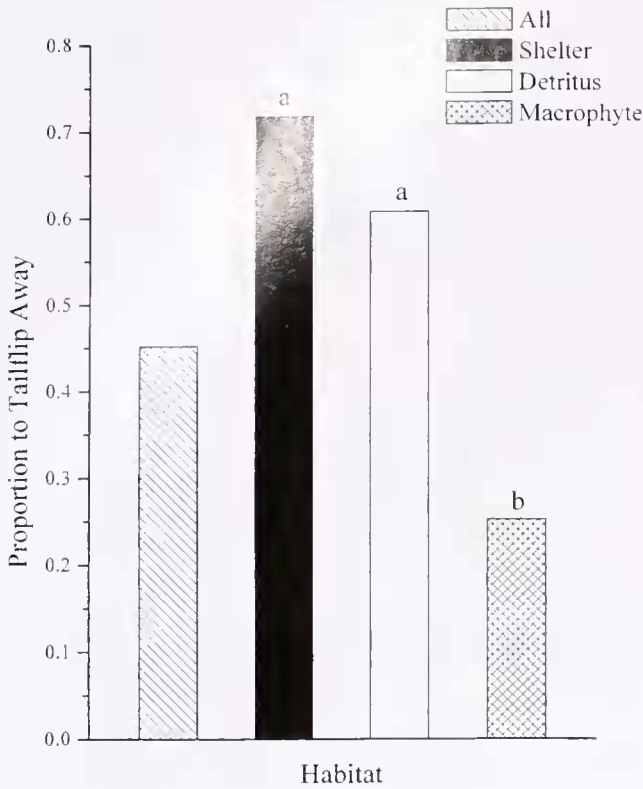
Figure 2. Frequency histogram showing the proportion of fights that ended in a tailflip for all fights (hatched), fights near shelters (black), fights on detritus patches (white), and fights among macrophytes beds (crosshatch). The letters above the bars denote a significant difference between the habitat types (contingency table for multiple comparisons of proportions; $P < 0.05$).

Figure 3. (A) Frequency histogram showing the proportion of fights that achieved each maximum intensity level for all fights (hatched), fights near shelters (black), fights on detritus patches (white), and fights among macrophytes beds (crosshatch). The letters above the bars denote a significant difference between the habitat intensities (contingency table for multiple comparisons of proportions; $P < 0.05$). (B) The average maximum fight intensity level achieved per habitat type. The letters above the bars denote a significant difference between the average maximum intensity per habitat ($P < 0.05$).

imum intensity level of 2 (meral spread display) than either encounters in the shelter (0.0; $q = 44.31$; Power = 1.00) or detritus habitat (0.36; $q = 14.86$ Power = 0.21) ($P < 0.05$; Fig. 3A). A significantly greater proportion of encounters on detritus patches reached the maximum intensity of 2 than did encounters in the shelter habitat ($q = 16.57$; $P < 0.05$; Fig. 3A). A maximum intensity of 3 (pushing with chelae) was reached in a significantly greater proportion of fights when in the shelter (0.67; $q = 22.01$; Power = 0.62) and detritus habitats (0.61; $q = 13.99$; Power = 0.11) than in macrophyte beds (0.15; Power = 0.62) ($P < 0.05$; Fig. 3A). There was no significant difference between fights in the detritus and macrophyte habitats ($q = 1.89$; $P > 0.05$). In addition, maximum intensity 4 (open chelae use by grabbing) was reached by a greater proportion of conflicts in the shelter habitat (0.33; Power = 0.24) than by interactions on detritus patches (0.03; $q = 11.23$; Power = 0.15) or macrophyte beds (0.0; $q = 20.0$) ($P < 0.05$; Fig. 3A). There was no significant difference between the detritus and macrophyte fights ($q = 2.83$; $P > 0.05$). No fights in any habitat achieved intensity 5 (unrestrained fighting). Encounters in the shelter habitat had a significantly higher average maxi-
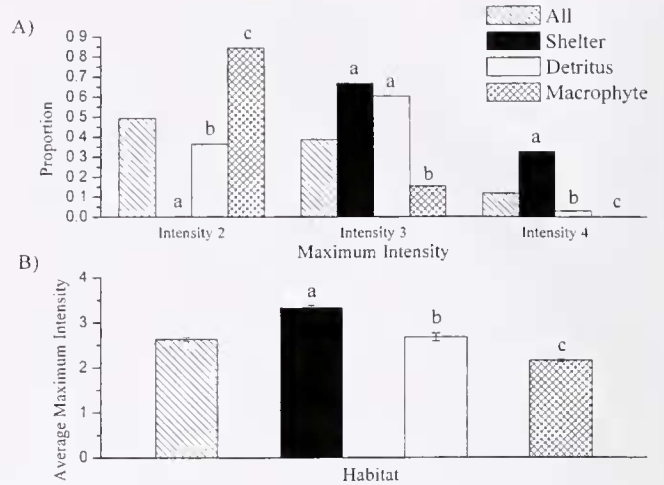
mum intensity (3.33 ± 0.05) than encounters in either of the other two habitats ($P < 0.05$; Fig. 3B). Interactions on detritus patches had a significantly higher average maximum intensity (2.67 ± 0.09) than encounters on macrophyte beds (average maximum intensity of 2.16 ± 0.03) ($P < 0.05$; Fig. 3B).
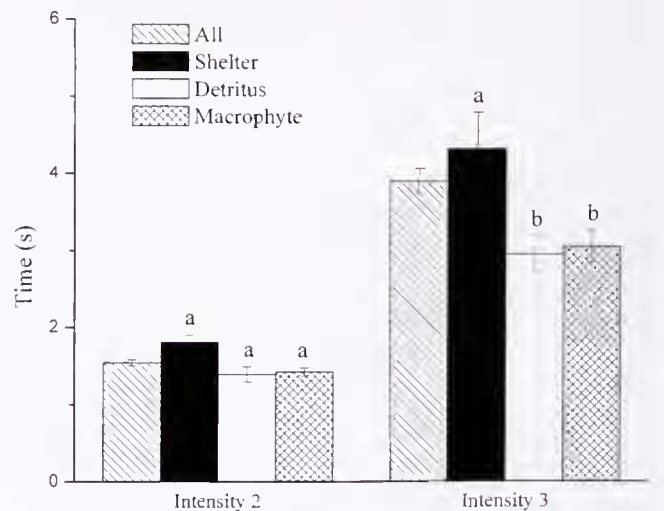

Figure 4. The mean (±SEM) time to intensity levels of all fights (hatched), fights near shelters (black), fights on detritus patches (white), and fights among macrophytes beds (crosshatch). The letters above the bars denote a significant difference for the time to reach intensity levels for each habitat (one-way ANOVA Tukey hsd *post hoc* test; $P < 0.05$).

Rate of escalation

The average time to intensity 3 was significantly longer in the shelter habitat (4.3 ± 0.5 s) than on the detritus patches (3.0 ± 0.2 s) or macrophyte beds (3.1 ± 0.2 s) (*P* < 0.05; Power = 1.00; Fig. 4). Intensity 2 showed no significant difference among the habitats, whereas intensity 4 was primarily achieved in the shelter habitat; however, no statistical test could be performed because of the lack of fights in the macrophyte (*n* = 0) and detritus (*n* = 1) habitats.

Effect of size differential on fight duration

A significant exponential regression analysis using the least-squares method demonstrated that the duration of agonistic interactions (*n* = 117) was longer when the size differential between opponents was smaller (*P* < 0.05; Fig. 5). Encounters were longer when opponents were size-matched within 10%, whereas fights with a size difference greater than 10% did not exceed 4 s.

Discussion

Extrinsic and intrinsic factors of agonistic behavior

Crayfish agonistic interactions were longer (Fig. 1A), more intense (Fig. 3A, 3B, 4), and more likely to end with a tailflip (Fig. 2) when the interaction took place near a shelter (burrow) than on or near food-resource habitats (detritus and macrophytes). Interactions in the shelter habitat were more likely to reach higher intensities, but they also took longer to reach those intensities (Fig. 4). These results indicate that shelters were more valuable than either

Figure 5. The percentage size differences of agonistic opponents analyzed with an exponential regression using the least-squares method. Size-matched fights lasted longer than fights between unevenly sized opponents (*P* < 0.05).

macrophytes or detritus patches. Shelters may be alluring because of their use to attract mates or in defense from predators (Hill and Lodge, 1999). Conflicts were more intense (Fig. 3A, B) and ended more often with a tailflip (Fig. 2) when they occurred on detritus patches as opposed to macrophyte beds.

Extrinsic factors, such as the availability of a shelter or a food resource, seem to influence aggressive fighting behavior in crayfish. With reference to food resources, when crayfish are fed a strictly macrophyte diet (*Amnicola* sp. and *Lymnaea* sp.) they have slower growth rates and higher levels of mortality than crayfish fed detritus (Hill *et al.,* 1993). Physiologically, it appears as if detritus is more nutritious and thus a more valuable resource than macrophytes. Moreover, crayfish have been observed foraging on both species of macrophyte (*Potamogeton* sp. and *Vallisneria* sp.) and on detritus, suggesting that all three are viable food resources (Lodge and Lorman, 1987; Hill *et al.,* 1993; Cronin *et al.,* 2002). Among these food resources, detritus was located in distinct patches, whereas the macrophytes and their associated epiphytes were far more abundant and consistently distributed in Burt Lake. Moreover, shelters and detritus patches are limited resources, hence more easily defended. Conversely, macrophyte beds are usually an easily accessible and abundant food source (Capelli, 1982), and defense becomes difficult and unnecessary when they are widely available. Given the increased nutritional value and limited distribution of detrital food sources, we predict that intraspecific encounters on detritus patches would be more intense and longer than fights in a macrophyte habitat. Indeed, in our sample, intraspecific fights lasted longer, reached a higher average maximum intensity, and ended more often with a tailflip. These results may be caused by the relative scarcity and temporal unpredictability of detritus patches within Burt Lake. Patches are often destroyed or moved overnight by physical wave action. Detrital patch heterogeneity may limit this potential nutritional resource, and when a crayfish finds a rare patch, the interactions become more intense in defense of it. In contrast, the macrophyte beds and their associated epiphytes had a more homogeneous distribution and greater temporal stability than detrital patches. As a result, macrophytes interactions were the least intense of the habitat types.

Our results for the crayfish interactions in the macrophyte and detritus habitats are consistent with the idea that detritus is more valuable than macrophytes because of its increased nutritional value (Hill *et al.,* 1993). However, no definitive conclusion about the relative merits of detritus and macrophyte diets can be drawn from our study due to the unknown and varying composition of the detritus. Nevertheless, both macrophyte and detritus food resources appear to be less valuable than shelters. Shelters have been shown to have an effect on agonistic outcomes in that the previous owner is more likely to retain a shelter and initiate more interactions
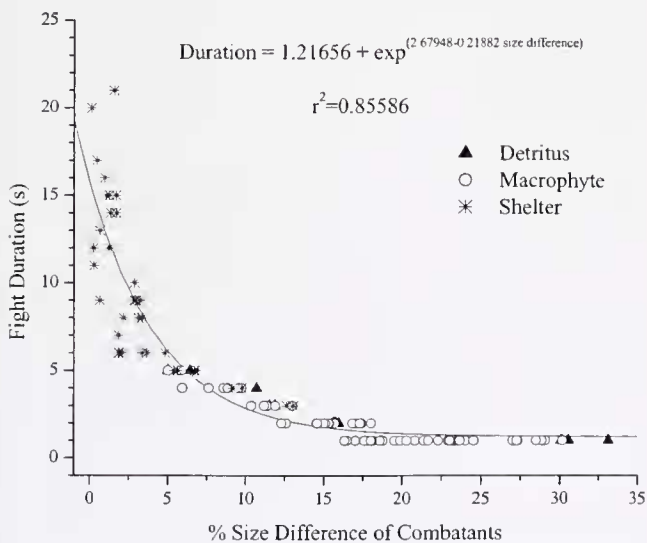
(Peeke *et al.*, 1995; Edsman and Jonsson, 1996). Capelli and Hamilton (1984) have shown that food and prior residencies affect agonistic behavior in a simplified laboratory environment. They reported that aggressive activity decreases with the increased availability both shelters and food. In addition, they show the increase in shelter availability reduces aggression more than an increase in food availability. Thus, high food availability, more macrophytes than detrital patches, and low shelter availability would lead to more intense conflict over shelters, followed by detritus patches, and then macrophyte beds.

Conspecific conflicts can usually be thought of as a "limited war," in which serious injury is avoided (Maynard Smith and Price, 1973). However, conspecific conflicts between crayfish involve potentially lethal chelae that allow for an "unlimited war" with the possibility for more intense and lethal fights. High-intensity fights are common in a laboratory environment, largely because the opponents have been closely matched for size of carapace and chelae (Huber and Kravitz, 1995; Karavanich and Atema, 1998a, b). In nature, an advantage in size directly confers an advantage in resource holding power (RHP) to the larger individual. Parker (1974) noted that as RHP disparity (size difference) increases, conflicts become less intense and shorter. Both combatants may increase their overall fitness by minimizing the chance for injury and reducing energy expenditure from long and intense fights. The winners of such interactions gain access to more valuable resources such as mates, food, or shelters, while the losers reduce their risk of predation, minimize energy costs, and emigrate to find a new resource.

Our results are typical for asymmetric contests (Maynard Smith and Parker, 1976) in which a larger individual holds more valuable resources (shelters), and conflicts are longer when the opponents are size-matched. Moreover, when resource availability is asymmetrical, conflicts will generally be shorter when the least valuable resource—macrophytes in this study—is in dispute. The shelter habitat appears to have some significance tied to it because the longest fights were in this habitat, and these fights were the most closely size-matched (Fig. 5). The longest fights in all three habitats occurred when the opponents were within 10% of each other in size (Bruski and Dunham, 1987; Schroeder and Huber, 2001; Stocker and Huber, 2001; Bergman *et al.*, 2003). However, the shelter habitat appears to be more closely matched than the food resource habitats; consequently, the valuable resource (shelter) may attract larger individuals, which causes smaller individuals to move to the periphery or into other habitats (detritus and macrophyte). Moreover, a hierarchy has likely been established in the stable shelter habitat, whereas the macrophyte and detritus habitats do not provide the same temporal stability and do not function to·decrease predation. The recognition of hierarchical status is probably reinforced by visual or chemical social or individual recognition of conspecifics (Bruski and Dunham, 1987; Karavanich and Atema, 1998a, b). Intrinsic factors, such as size and recognition, and extrinsic factors, such as environmental surroundings, are important in determining intraspecific agonistic outcomes. However, the extent of the role each intrinsic and extrinsic factor plays is yet to be conclusively determined.

Cursory review of laboratory studies in relation to field observations

Intraspecific aggressive behavior between decapod crustaceans can be influenced by a myriad of extrinsic factors. For example, an extrinsic factor such as small aquarium size will sometimes elicit a "critical reaction" (Hediger, 1950). A critical reaction occurs when antagonists are crowded together in an aquarium with no possibility of escape. The inability to escape a competitor can cause changes in fight duration, retreat behavior, and intensity levels reached in fights (Peeke *et al.*, 2000). The presence of a defendable extrinsic resource can also cause an escalation in fight intensities in small aquaria. When shelters are present, fights will be more intense than when they are absent (Peeke *et al.*, 1995). Intrinsic factors such as size, sex, and social experience can also affect aggressive activities. Size-matched large crayfish escalate more slowly to high intensities and have longer fight durations than size-matched small crayfish (Schroeder and Huber, 2001). Generally, male crayfish are more aggressive than females (Bruski and Dunham, 1987), and social experiences in the form of winner and loser effects influence the likelihood of success in subsequent fights (Daws *et al.*, 2002; Bergman *et al.*, 2003). These extrinsic and intrinsic factors change the dynamics of fights in the laboratory so that they do not necessarily show the same characteristics as fights in a natural setting.

In general, fights were shorter (5.3 ± 0.4 s; Fig. 1) and had lower average maximum intensities (2.6; Fig. 3B) in the field than in laboratory studies (Table 2). The average maximum fight intensity in the field was lower than in laboratory fights seen by both Schroeder and Huber (2001) (2.7 and 2.8) and Bergman *et al.*, (2003) (4.2 and 3.5) (Table 2). In addition, the time to different intensity levels has been used as a measure of the rate of escalation in violence during fights and was considerably shorter for all intensities in the field than in the laboratory fights of Stocker and Huber (2001) and Bergman *et al.* (2003) (Table 2).

Within a laboratory environment, all aspects of a confrontation can be controlled to lengthen conflicts or increase fight intensities. Sex, species, size of opponents, size of aquarium, reproductive state, status/individual recognition, social experience, and hierarchy establishment can all be controlled in the laboratory. An example of a controlled variable is size-matched opponents (Bruski and Dunham, 1987; Rutherford *et al.*, 1995; Stocker and Huber, 2001;

Table 2

Cursory review of crustacean agonistic experiments in the laboratory

Reference	Animal	Treatment	Duration (s)	Avg. Intensity Value	Time to Intensity 2	Time to Intensity 3	Time to Intensity 4
Bergman and Moore (This study)	Crayfish	Field observations	5.3	2.6	1.5	3.9	9.5
Bergman et al., 2003	Male crayfish	Previous win experience vs. size-matched opponent	127.0	4.2	4.6	8.6	18.0
	Male crayfish	Previous win experience vs. size-matched anosmic opponent	452.0	3.5	87.0	72.0	336.0
Stocker and Huber, 2001	Satiated male crayfish	Food odor present; Size-matched	—	—	85.0	135.0	210.0
	Starved male crayfish	Food odor present; Size-matched	—	—	60.0	90.0	125.0
Zulandt et al., 2001	Familiar male crayfish	Urine present; Fight 1/Fight 2	80/70	1.9/1.8	—	—	—
	Familiar male crayfish	Urine absent; Fight 1/Fight 2; Size-matched	230/80	2.4/2.0	—	—	—
Schroeder and Huber, 2001	Male crayfish	Small; Size-matched	16.7	2.7	—	—	—
	Male crayfish	Large; Size-matched	30.6	2.8	—	—	—
Guiasu and Dunham, 1998	Male crayfish	First fight/Last fight; Size-matched	95.3/46.2	—	—	—	—
Guiasu and Dunham, 1997	Male crayfish	First fight/Last fight; Size-matched	115.6/26.2	—	—	—	—
Bruski and Dunham, 1987	Male crayfish	Dark; Size-matched	42.0	—	—	—	—
	Male crayfish	Light; Size-matched	17.0	—	—	—	—
	Female crayfish	Dark; Size-matched	29.0	—	—	—	—
	Female crayfish	Light; Size-matched	11.0	—	—	—	—
Karavanich and Atema, 1998a	Male lobster	Control; Day 1 Size-matched	510.0	—	—	—	—
	Male lobster	Control; Day 2 Size-matched	150.0	—	—	—	—
	Male lobster (anosmic)	Anosmic; Day 1 Size-matched	350.0	—	—	—	—
	Male lobster (anosmic)	Anosmic; Day 2 Size-matched	525.0	—	—	—	—
Huber and Kravitz, 1995	Male and female lobster	Day 1; Size-matched; Laboratory-raised juveniles	568.0	—	—	—	—
	Male and female lobster	Day 2; Size-matched; Laboratory-raised juveniles	365.0	—	—	—	—

Bergman *et al.*, 2003). Size matching increases the likelihood that fights will be longer and more intense than usually observed in the field. Field encounters had an average fight duration of 5.3 s (Fig. 1), whereas crayfish fight durations in the laboratory ranged from an average of 11.0 to 452.0 s (Bruski and Dunham, 1987; Bergman *et al.*, 2003) and lobster interactions took longer yet, ranging from 350.0 to 568.0 s (Huber and Kravitz, 1995; Karavanich and Atema, 1998a) (Table 2). This study does show that the fights of closely size-matched individuals are longer than those of unmatched opponents (Fig. 5), but they are not as long as fights seen in the laboratory. A possible extrinsic influence on this increased duration of fights is confinement of animals within an aquarium. Within the laboratory, a push to use larger aquaria will reduce the "critical reaction" effect

on fights by providing space for a possible escape that signifies the end of a conflict. Generally, the dynamics of laboratory fights tends to mimic field observations. However, Guiasu and Dunham (1997, 1998), using relatively large aquaria, showed average fight durations of 115.6 and 95.3 s, times that are considerably longer than those seen in this study (Table 2). The light regime also affects the duration of crayfish fights. Crayfish fights are shorter in the light than in the dark (Bruski and Dunham, 1987; Table 2). However, under different circumstances, fights can reach very long durations under lighted conditions, as was observed by Zulandt Schneider *et al.* (2001) and Bergman *et al.* (2003) (Table 2). One cannot discount the fact that laboratory conditions may have an unknown effect on agonistic behavior.

Summary

These field observations sugge   ia: the environmental surroundings have a significant .   .i on intraspecific ago- nistic bouts in crayfish. A-   sted by Parker (1974), asymmetries in resource-l   power can be an important factor in fight progr   conflicts in the presence of shelters were longer and more intense, suggesting that shel- ters have a higher fitness value than detritus or macrophyte food resources. A shelter's protective value may outweigh the value of the food sources when the threat of predation is especially high. Detrital food sources are likely more valu- able than macrophyte food sources because of their patchy distribution and the nutritional inadequacy of macrophytes (Hill *et al.*, 1993). It is quite evident from this study's results that extrinsic resources are an intricate influence on the agonistic interactions of crayfish.

Moreover, we conclude that aggressive behavior must be examined both in the laboratory and in the field to better understand the factors that influence crayfish aggression. Each experimental environment has unique benefits and problems. Observations in nature contribute to an under- standing of habitat usage, movement patterns, shelter occu- pation, and food availability. Laboratory experiments are invaluable in elucidating the behavioral mechanisms and the environmental components that affect aggression. By con- trolling different aspects of agonistic interactions, such as size, sex, food preferences, and shelter accessibility, a re- searcher can test facets of agonistic behavior that are not easily controlled in a natural setting. However, such inves- tigations do not answer the question of whether the behavior is an artifact of laboratory confinement or a behavior that is displayed in nature. Consequently, one must be hesitant when using laboratory results to explain agonistic behaviors in the wild. Laboratory and field observations show consid- erable differences in fight dynamics. A combination of the two is needed to develop a realistic picture of aggressive behavior.

Acknowledgments

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